

PROMISING DIRECTIONS OF STUDY IN TROPICAL ANIMAL-PLANT INTERACTIONS¹

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Plants are not just food for animals, and animals are not just decorations on the vegetation. The world is not green. It is colored lectin, tannin, cyanide, caffeine, aflatoxin, and canavanine. And there is a lot of cellulose thrown in to make the mix even more inedible. Animals are not ambulatory bomb calorimeters. They starve, they ache, they abort, they vomit, they remember, they die, and they evolve. Peter Raven asked me to write about promising directions in tropical animal-plant interaction studies, mostly because he believes there are some. Well, it's roughly analogous to standing in the city of London after WWII and saying, well, let's get on with studying the promising directions in London's architectural history.

My paper is about tropical interactions; they are the first to be extinguished by man's onslaught and the last to be lamented. Interactions have several traits that make them especially inconspicuous (Janzen 1974a). (a). The participants, being to some degree self-sufficient, may persist well after the interaction that produced them is gone; a *Scheelea rostrata* palm left standing in a Costa Rican pasture will persist long after the agouti that buried its seed and the forest that gave dry season shade to its seedlings has been removed (Janzen 1971a). (b). Humans eat participants, not interactions; being relatively incompetent until quite recently, humans have by and large not generated cultural rules for the maintenance of interactions per se, but rather for the preservation of the participants. (c). Humans eat only certain participants, and often atypical ones; if the interaction is to be preserved, it is not the overall interaction in which the participant happens to be imbedded that is preserved, but rather that subinteraction which will generate the largest number of participants for dinner. (d). The systematics and taxonomy of interactions is hopeless; most of the types have already been mutilated or destroyed and what is perhaps even worse, it is virtually impossible to look at an interaction and know if it is largely intact. (e). You cannot collect an interaction and keep a specimen on display in a museum. (f). An interaction has no material potential worth, as opposed to the participants which can be noticed and retained if for no other reason than the optimistic view that some day a use may be found for one of them. However, and this is a big however, I must add in the same breath that it is as examples of how things can happen that interactions are the most valuable and therefore most deserving of preservation. The big problem is that human wants are generally so unrepresentative of organisms in general; the specific interactions desired by humans are not

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likely to be found in nature but rather will have to be hand-tailored with the desired participants.

Now after that pessimistic preamble, I am still left with the task of pointing at some promising directions in the study of tropical animal-plant interactions. There are many. I take them in no particular order, and if I ignore one of particular importance to you, view it as oversight and not an evaluation. Rather than preach that we should study this or that, I will simply give brief examples to draw attention to mysterious patterns, curious new hypotheses, and perplexing observations. Gilbert (1977) has, on the other hand, presented somewhat of a challenge when he stated that "It is not clear, however, that further base-level exploration would provide many new ecological or evolutionary insights, or that additional categories of interactions would be found which fall outside those major kinds that have so far been described." I wonder.

Any person seriously interested in tropical animal-plant interactions should take a week or two to read the recent symposium and review publications in this area (Van Emden, 1973; Luckner et al., 1976; Burley & Styles, 1976; Gilbert & Raven, 1975; Wallace & Mansell, 1976; Jermy, 1976; Levin, 1976; Gilbert, 1977) and browse the numerous papers on this subject in the post-1969 issues of *Ecology*, *American Naturalist*, *Science*, *Biotropica*, *Oecologia*, *Journal of Animal Ecology*, *Journal of Applied Ecology*, *Evolution*, and the *Annual Review of Ecology and Systematics* (among others).

PLANT PRODUCTIVITY AND THE ANIMALS IN THE HABITAT

At the lowland Pasoh rain forest, Negri Sembilan, Peninsular Malaysia, I censused the plants in flower that were less than 3 m tall in the understory of undisturbed forest along 3 km of narrow trail (early September, 1976). I found one orchid, one 1.5 m tall Araliaceae, one 0.5 m tall Acanthaceae (*Lepidagathis longifolia*), and one 1 m tall *Ixora*-like Rubiaceae. In the lowlands of the national park, Taman Negara, 5.4 km of rain forest trail yielded one white-flowered ginger, two *Ixora*-like Rubiaceae, one Acanthaceae, one unknown family, and two 10–20 cm tall Gesneriaceae with underground stems. In primary forest understory in the new Corcovado National Park (20–160 m elevation, Osa Peninsula, southwestern Costa Rica), a trail-side survey of 4.3 km yielded 94 plants in flower of 18 species (20 November 1976). In other words, I averaged 1.3 plants in flower per kilometer in the Malayan rain forest understory and 21.9 plants in flower per kilometer of Costa Rican rain forest understory.

These woefully small samples reflect accurately my general impression of the general abundance of flowers in the understory of rain forests of Peninsular Malaysia and Sarawak, as compared with those of Costa Rican rain forest of similar elevation. I was informed locally that 1976 was one of the heaviest years in memory for flower and fruit production in Peninsular Malaysia; November is the time of most reduced flower production in Costa Rican rain forest understory (and see Frankie et al., 1974). In short, if one were to turn loose in Pasoh or Taman Negara the rain forest understory fauna of flower-visiting hummingbirds, butterflies, moths, and bees found in the Corcovado, I predict that they would be dead of starvation in a few days. Furthermore, they could not survive

by moving out into secondary regeneration; Malaysian disturbed sites have a grossly lower flower abundance than any weedy wet-season vegetation that I have seen anywhere in the African or neotropical lowlands.

Over the Malaysian transects mentioned above, I encountered 63 understory individuals in fruit (22 species) for an average of 7.5 per kilometer. In the Corcovado forest, there were 345 individuals in fruit (34 species) for an average of 78.4 per kilometer. Again, the fauna of understory birds that frequently eats small fruits in neotropical rain forests would have a very rough go of it in the Malaysian forests.

It is extremely interesting that after doing this and writing the above, I discovered Karr's (1976) statement that "about 80% of the canopy and understory tree species on Barro Colorado Island are dispersed by animals (Foster, 1973), while only about 10% of the trees on Fogden's (1972) [Sarawak] study area were important as sources of fruits for birds." Furthermore, at the IV International Congress of Ecology in Panama, Karr (March, 1977) noted that "The most striking difference is the total lack of undergrowth frugivores in mist-net samples taken from Malaysia as compared with 25–33% of the individuals captured in undergrowth of African and Central American forest."

I would like to propose a rather sweeping hypothesis to account for this paucity of flowers and fruits on rain forest understory shrubs, a paucity which should have a very depressing effect on the biomass and species richness of the understory fauna. I need first, however, to belabor you with three facts about the lowland Malaysian rain forests in which the censuses were made.

(a). They are dipterocarp forests, which means that between 50 and 80% of the tree crowns in the canopy belong to species of Dipterocarpaceae. The members of this family, in Malaysia and some other tropical Asian areas, mast fruit within (and between) habitats. Thus the bulk of the flower and fruit production by better than half of the upper canopy photosynthetic machinery is pulsed at 3 to 11 year intervals. Associated with this, the animal community is sufficiently satiated by the enormous numbers of seeds that a very large number survive to the seedling and small sapling stage (Janzen, 1974b).

(b). Malaysian rain forests, on the Malay Peninsula or in Sarawak, are largely perched on sandy soils ranging from very old white sand deposits (such as in Bako National Park, Sarawak) to very sandy soils derived from weathering of granitic base rock that has not been inundated by the sea for an extremely long time. There is no volcanic overlay nor crust of weathering limestone on the majority of the terrain. There are many indirect measures of the relatively low ability of these soils to generate a vegetation with a high harvestable productivity for other organisms: when cleared, the second-growth vegetation is very slow to refill the site (Janzen, 1974b, 1974c, and this is probably why plantation rubber is so successful on these soil types); the forest has largely remained uncut and unexploited by agrarian peoples despite their presence in the general area for many thousands of years (note that virtually all of nearby Java on volcanic soils is under agriculture); second-growth vegetation of the sites has an amazingly low insect biomass as compared to that of comparable neotropical weedy sites (Janzen, 1974b); etc.

(c). There *are* bees, butterflies, flower-visiting birds, small fruit-eating birds, etc. present in the Malaysian rain forests. In other words, pollinators and dispersal agents can be drawn from these groups if the ecological and evolutionary opportunity is presented.

I hypothesize that the shortage of rain forest understory flowers and fruits is largely attributable to two forces operating simultaneously and synergistically. First, I hypothesize that the large pulse of dipterocarp seedlings and saplings takes up a large part of the resources that are available to neotropical understory shrubs; the dipterocarp offspring are apparently dying in large part through competition rather than through supporting a seed-predator guild. Simultaneously, they are analogous to an enormous and very generalist herbivore in their impact on understory shrubs. Since dipterocarp seedlings never flower or fruit, they take a large portion of the understory resources without feeding part of it back into the flower-visitor and fruit-eater guild so conspicuous in a neotropical forest. Second, I hypothesize that as the soil conditions get progressively worse, the ability to be a reproducing individual in the light-poor understory is reduced. That is to say, irrespective of the presence of the dipterocarp seedlings, if the forest canopy is held constant and the soil fertility is depressed, the biomass (number of individuals in general) and reproductive output per ha by understory shrubs should fall (just as it would if soil fertility were held constant and the light were decreased). In other words, the rain forests of Malaysia sit on a poorer piece of real estate than do those of lowland Costa Rica, and the flower and fruit density in the understory reflects this.

The animals are probably woven into this matrix more firmly than I have indicated so far. I have hypothesized that the habitat-wide masting behavior of these Dipterocarpaceae is driven at present, and was selected for in the past, by the seed predators in general (Janzen, 1974b). Further, I have argued that the lower the overall productivity of the site, the more likely it is that the animals will select for masting behavior because the less food there is for them between mast crops, the more severely they are depressed in density by masting behavior. But the scarcer they are between mast crops, the fewer understory flower and fruit crops they can (will) visit; the fewer crops they visit, the less well off will be such plants and the better off will be the dipterocarp seedlings in competition with nondipterocarps. Why doesn't the system progress to where there are nothing but seedlings and saplings of overstory trees in the understory? Probably because as time passes since the last mast crop, competitive and accidental deaths clear the arena for some other species of plants, and because a number of animals that visit flowers in the understory can also go elsewhere for food; many frugivores can feed on insects and other food types when understory fruits are scarce.

The focus to this point has been largely on the biomass of flowers and fruits, and associated animals. However, the species richness of plants and animals should also be negatively influenced by a reduction in harvestable productivity (Janzen, 1977c). My argument involves resource partitioning and specialization on the partitions. In short, as the productivity of harvestable resources in the habitat falls, more and more resource blocks become too small to sustain a spe-

cialist. They are then taken by a more generalized harvester or by another trophic level. In the context of the example under discussion, the number of flower-visiting species of understory birds should decline as the soil gets poorer and as the overstory becomes progressively more synchronized at supra-annual seeding. For example, in a Costa Rican rain forest there are species and morphs (often females) of hummingbirds (e.g., *Phaethornis* spp.) that specialize on widely scattered understory individuals in flower, and species and morphs (often males) that specialize on large clumps of flowers on forest edges (e.g., Stiles, 1975). From what I have seen of Malaysian lowland rain forest, a hummingbird would have to forage at all such sites and then some to stay in the game. Simultaneously the species richness of seed predators in the habitat should also decline as soils become poorer and synchrony increases, since the progressively more pulsed nature of the seed resource makes it effectively scarcer in any but the very exceptional mast year. For example, in a Costa Rican rain forest there is a large standing crop of agoutis (*Dasyprocta punctata*) and pacas (*Cuniculus paca*) that live on the rather continuous input of fruits, seeds and young seedlings (e.g., Smythe, 1970). These animals are relatively sedentary. They do not have ecological analogues in Malaysian forests, and I suspect the reason to be that in most years the seed resource is not large enough to sustain them, though in mast years it is far greater than they could ever consume before the seeds germinate.

The pulsing of productivity in a rain forest can have other interesting side effects on animals. It should select for migratory or very nomadic species, which are in turn less likely to develop local regional populations than are more sedentary species. I have argued that the wind-dispersed nature of dipterocarp seed (and that of other trees that fruit as they do, such as the legume *Koompassia*) is due to their specialization to the site on which their parent grew and is not involved in escape from seed predators through dispersal (Janzen, 1977d); it may also be due to an extreme shortage of biomass of frugivorous animals owing to the fact that much of the seed production by the forest is pulsed (the frugivores would be severely satiated on seeding years, just as would be the seed predators). Whatever the cause, the fact that most of the canopy-level seed production is wind-dispersed eliminates a large portion of the fruit input that is an important part of the diet of many neotropical animals. For example, I doubt very much that any Malaysian forest comes anywhere close to the figures of 1.93 g of fruit per m² calculated to fall in a Panamanian rain forest by Smythe (1970). However, in closing this paragraph, I cannot help but notice that Malaysian forests have an exceptionally high number of species of squirrels (e.g., 19 tree squirrels in Borneo; Davis, 1962). It is possible that squirrels are particularly good at dealing with a highly pulsed food input, as compared with the other animals that eat seeds and fruits (some in fact, are specialists on insects or vegetative parts of plants). In short, as harvestable productivity becomes progressively less available, there is no reason to expect all animal life forms to be depressed at the same rate. In fact, the elimination of some could quite reasonably result in an increase in others.

The ramifications of low productivity of harvestable resources by the plant

community in an average year can produce a multitude of higher-order interactions. For example, in 17 days of fieldwork and travel between field sites by boat or small car, I saw a total of three raptorial birds in Peninsular Malaysia (and none in 11 days in Bako National Park, Sarawak). The area traversed was at least 480 km of urban, rural, and forest roads, 122 km of large river through farmland and forest reserve (Tembeling River on the way to and from Taman Negara), and about 50 hours of hiking in forest reserves. At least 80% of the weather was nonrainy. I should emphasize that I was not searching for raptorial birds, but rather just watching for any kind of animal. In a similar excursion up and down the similar-sized Sanaga River in Cameroun, I took photographs of 23 birds of prey and saw at least 50 more. In Ugandan and Kenyan forest-farmland and national parks, it is hard to find a moment on a clear day when a raptor or large avian scavenger is not in view somewhere (and see Janzen, 1976a). In Costa Rican lowland rain forests, forest-farmland mixes, and open pasturelands, raptors and/or scavengers are seen at least once every several hours, and much more often in many circumstances.

The ornithological literature is not designed so as to provide material relevant to comments such as those above. However, a few interesting tidbits can be extracted. For example, the black or king vulture (*Torgos calvus*) is common throughout the northern part of the Malay Peninsula but is almost never seen in the southern half (rainforested portion) of the peninsula; the same may be said of the other peninsular vulture (*Pseudogyps bengalensis*) (Robinson, 1927; Medway & Wells, 1976). As Wells put it (personal communication), there is no vulture (for all practical purposes) in West Malaysia. The standard explanation for the absence of vultures is Robinson's (1927) comment that "securing their food entirely by sight, it is obvious that a heavily forested country is quite unsuited to them and it is for this reason, probably, that they do not extend to the Malay Archipelago." This seems to me to be a quite inadequate explanation. As Peninsular Malaysia has been cleared, vultures have become rarer, not more common (Robinson, 1927). Furthermore, one has to ask (1) why similarly heavily forested areas in other parts of the tropics sustain vultures, (2) why the forest was not cleared for agriculture and livestock long ago as it was in other parts of the tropics, and (3) why the contemporary invasion of agricultural peoples does not bring with it adequate food for vultures? In short, I hypothesize that rain forest Peninsular Malaysian and Sarawak habitats never did generate enough carrion to keep vultures in the game, and that the contemporary peoples occupying these habitats cannot raise enough livestock to generate enough spin-off carcasses for vultures to persist as the land is cleared. Central American rain forest and associated natural disturbance sites, when put into multi-use agriculture and livestock husbandry, sustain conspicuous populations of three species of vultures and two caracaras (hawks that act like vultures).

I doubt that the paucity of vultures or vulturelike birds in Malaysia is due to excessive hunting; however, if there is less food for them, then even small amounts of hunting can do disproportionately more damage than if there is a large resource base. I doubt that the large varanid lizards, relatively common on riverbanks and in refuse dumps where not hunted, are competitively exclud-

ing the vulturelike birds. I saw 28 large (0.5–1 m snout–vent) *Varanus* along the bank of about 20 km of the Tembeling River at and below Taman Negara on one morning. Rather, I suspect that the absence of vultures allows the presence of these relatively slow scavengers; if the food is scarce and occurs at very long intervals, then a cold-blooded professional starver would be able to maintain a much higher biomass than birds. I was told by a Kuala Lumpur “pet” dealer that with water, a large varanid can live a year without food; I doubt a vulture could do the same.

The hypothesis that the natural habitats of West Malaysia generate a low density of food for large carnivorous birds is also supported by the species richness of falconids and accipiters. West Malaysia has 11 resident species of accipiters and 1 resident falcon (Medway & Wells, 1976) and is about 132,000 km² in area; Costa Rica has at least 28 resident species of accipiters and 8 resident falcons and is 51,000 km² in area (Slud, 1964). The tiny Costa Rican rain forest field station at Finca La Selva (6.1 km²) has at least 9 resident accipiters and 4 resident falcons (Slud, 1960).

Hérons, bitterns, and egrets are conspicuously scarce in fields, roadside ditches and impoundments, rice paddies, streams, marshes, and riverbanks in West Malaysia away from the sea. I did not see a single individual in the 17 day field period. More specifically, not a single one was seen along the 122 km traversed of the Tembeling River, despite careful search for them. These birds are conspicuous in similar habitats in Africa and Central America. On the Sanaga River trip mentioned above, I photographed 7 species and saw at least 30 individuals. Such birds are a standard part of the scenery along large Central American rivers and in the kinds of habitats mentioned at the beginning of this paragraph. Inquiry of ornithologists in West Malaysia produced two useful comments. First, “they are absent because they don’t migrate here”; well, what is wrong with West Malaysian real estate so that migrating large piscivorous birds don’t use it much as overwintering grounds? Second, “these birds are conspicuous in areas near the sea.” For example, Medway & Wells (1976) noted that 6 of the 9 resident species of Malayan Ardeidae are associated with mangroves. If in fact West Malaysia is a poor habitat for these birds, then the mangroves and river deltas should be the best of the sites, and appear disproportionately good compared to inland areas. Again, tiny Costa Rica has 14 species of resident Ardeidae (Slud, 1964) to compare with 9 for Peninsular Malaysia (Medway & Wells, 1976).

I hypothesize that herons, bitterns, egrets (and anhinga- and cormorant-type birds) are in short supply in the West Malaysian inlands simply because the waterways don’t generate enough biomass of aquatic food for them. If the surrounding terrestrial habitats generate a reduced number of insects as well, which are an important part of the diet of many ardeids, the effect would be compounded.

The biomass of vascular epiphytes in the crowns of rain forest canopy-member trees at low and intermediate elevations is conspicuously lower in dipterocarp forests than in analogous rain forest in Costa Rica, Venezuela, Colombia, Cameroun (Edea Forest Preserve), and Uganda (near Fort Portal). The

quantity of bare horizontal large branches in the canopy of a forest such as that at Pasoh or Taman Negara is phenomenal.

I hypothesize that the cause is that the habitat generates such weak nutrient rain (bird droppings, dead insects, ant nest debris, rainwater minerals, dust, leaf and fruit litter, leachate from living tissues) that the epiphytes are starved off the tree. In short, I suspect that it is a general example of the extreme case at Bako National Park, Sarawak; here, on a white-sand soil area, the only surviving epiphytes on upland trees were those associated with the nutrient-gathering activities of an ant colony (Janzen, 1974c). There are several conspicuous alternative hypotheses as to why there is a shortage of vascular epiphyte biomass as compared to neotropical rain forest.

(a). The bromeliads (Bromeliaceae) never made it to the Malaysian tropics and it is their absence that makes epiphyte biomass seem so low. Such a hypothesis does not explain why epiphytic orchids, gesneriads, ferns, asclepiads, Piperaceae, ericaceous shrubs, rubiaceous shrubs, etc. are equally low in biomass.

(b). The Dipterocarpaceae, which make up 30 to 90% of the crowns in the canopy of the forests I examined, have evolved bark traits inimical to epiphytes. It is certainly possible for this to occur, as there are species of neotropical rain forest trees that regularly have crowns clean of epiphytes while growing only a few feet from many species festooned with epiphytes. However, if this is the explanation, it is many more species of tree than just those in the Dipterocarpaceae that have perfected their anti-epiphyte defenses. It seems unlikely to me that a whole flora of large trees could evolve this ability. Furthermore, if nutrients are exceptionally scarce for epiphytes, then even weak defenses may be adequate to keep them off.

There are two observations that are relevant to this hypothesis. On rare occasions I did encounter a native tree that was solidly covered with large epiphytes. For example, there is a medium-sized tree on the bank of the Tembeling River about halfway between Tembeling and Taman Negara that has hundreds of plants of a large basket fern on it (though perhaps it might be one huge clone linked by rhizomes). I saw no other individuals of this fern on the trees along the river. How does a huge plant like this one stay in the game as an epiphyte? It is possible that its litter-capturing leaves have an exceptionally robust ant colony living in them, or that its substrate tree is one of the few epiphyte-susceptible species in the region. Second, when Central American trees such as *Pithecellobium saman* (rain tree) or mahogany (*Swietenia* spp.) are planted in Malaysia, they develop large epiphyte loads. However, all the examples I saw were growing in small villages or roadsides where one would expect dust and other debris to provide high quality aerial fertilizer for the epiphytes. It is notable that these trees are deciduous forest trees in Central America and when transplanted to the evergreen forest within their native country, they also develop exceptionally high epiphyte loads, even for the rain forest.

In closing this section, let me call your attention to a quite different set of habitats where there appears to be a relationship between animal species richness and harvestable productivity. On Costa Rican and Venezuelan mountain-side gradients, rather than the species richness of insects in sweep samples falling

off linearly with increasing elevation, it actually increases or at least stays about the same up to about 1,000–1,600 m elevation (Janzen, 1973a, Janzen et al., 1976). I have hypothesized that this “mid-elevational bulge” is the result of a similar bulge in harvestable productivity that occurs in the following manner. As one rises in elevation, the nights become cooler but the day does not cool as rapidly, and thus photosynthate production does not decline as rapidly as does nocturnal respiration. The result should be a greater amount of net produce per unit time for the plant, until an elevation is reached where diurnal photosynthesis is also severely reduced.

If this is actually going on, should it result in an increase in numbers of *species* of herbivorous insects? I would argue yes, because as I have argued earlier, there should be more fractions of each plant species (e.g., the new shoot tips produced in the lower outer third of the crown) that are large enough to support a specialist herbivore. By like reasoning there should be an increase in the species richness of arthropod predators and parasites of these insects (Janzen, 1973a, 1977c). The more generalized a feeder (e.g., birds as contrasted with parasitic Hymenoptera), the less a taxonomic group should be affected, but all should be affected somewhat. Moving in the other direction, should the increased photosynthate production result in more species of plants than expected with a straight-line relationship between elevation and harvestable productivity? Yes, but again to a lesser degree than with the herbivores. By increasing net photosynthate to an individual plant, there will be some kinds of specialization in which it can now participate (and thus more species can be packed into the habitat), but the relative heterogeneity of the increased photosynthate should be low compared to that received by the herbivore; the resource called sunlight is subdivided into many fewer compartments than the resource called “those plant parts that a herbivore eats.”

By these varied examples I mean to suggest that a very promising yet unexplored area in tropical animal-plant interactions is the relationship between the pattern and amount of harvestable productivity and the numbers and kinds of animals present, and vice versa. We badly need solid data on relative abundances of animals and rates of production of harvestable parts of plants, collected with reference to particular questions such as “Given foraging inefficiencies and temporal distribution requirements, how much small bird biomass can be supported by the understory fruits of Pasoh rain forest?” Or, “Do mid-elevation plants replace shoot tips faster than their analogues at low elevations?”

MONOCULTURE FORESTS

In worrying about tropical forests, the intellectual interest of ecologists and population biologists has been largely focused on the “Oh My” habitats containing many species of trees (e.g., Ricklefs, 1977; Janzen, 1970; Connell, 1971; Ashton, 1969; Grubb, 1977). However, what I find much more perplexing are the lowland tropical forests with extremely low species richness of large trees: *Shorea albida* peat swamp forests in Sarawak (Anderson, 1961, 1964); *Mora excelsa* forests in Trinidad (Beard, 1946; Rankin, 1977); *Ocotea*, *Mora*, and *Eperua* forests in Suriname (Richards, 1952); *Gilbertiodendron dewevrei* forests

in West Africa (Gérard, 1960); mangrove forests around the world (Watson, 1928); *Strobilanthes* forests in the Asian tropics and bamboo forests around the world (Janzen, 1976b); *Raphia taedigera*, *Pterocarpus officinalis*, *Prioria copai-fera*, and *Parkinsonia aculeata* swamp forests in Costa Rica (Janzen, 1977b and unpublished). For the mercenary at heart, esoteric ecological studies of these sites and their plant-animal interactions should tell a very great deal about the art of growing monocultures of tropical trees without a large input of pesticides, herbicides or other costs. Perhaps instead of worrying about the return to nature through the reinvention of mixed stands, which is so much in fashion these days, we should be studying much more intensely those species that naturally occur as pure stands. Not that I am eager to see this information become part of the foresters' operating protocol, however, unless it is accompanied by a (unlikely) kick-back to biology in the form of inviolate forest preserves.

The questions these pure stands bring to mind are numerous, and here I mention just a few.

(a). From whence come the pollinators when a large pure stand suddenly comes into flower, a pure stand that has had little or no flowering activity for one to several years? In general, these monocultures are adjacent to much more mixed stands of plants, and I suspect that it is from these stands that they draw most of their pollinators (though bamboo use wind and *Strobilanthes* use highly nomadic bees; Janzen, 1976b). In the specific case of Dipterocarpaceae, which form a "monoculture" of sorts in Malaysian forests if the entire family is viewed as a species, Ashton and his associates have found that the enormous quantities of flowers suddenly produced are probably pollinated by thrips (Ashton, personal communication), and I suspect that these insects feed on the vegetative parts of dipterocarps or other plants during the intervening years. Further, being very small, thrips can have a very high rate of population growth; the flowering season for dipterocarps as a whole is 4 to 6 months in length and thus there can be an extensive population explosion of thrips. Finally, it appears that the flowering times of the different dipterocarp species are scattered through the overall flowering time (in contrast to the highly synchronous fruit drop over about 2 months), and I suspect that this is the result of interspecific competition for pollinators (Janzen, 1977d).

(b). In every monoculture stand of tropical forest known to me, the usual dispersal of seeds is by falling below the parent, variously aided by wind; thus a shortage of dispersal agents would not appear to be a problem for these plants. However, this kind of dispersal means that a near neighbor is likely to be a sib, mother, grandmother, etc., and that outcrossing is therefore more difficult than in a population whose seed shadows overlap widely due to animal dispersal of seeds. But then again, in a permanent monoculture, perhaps the best genotypes are extremely specialized to that site, and thus genotype disruption or offspring heterogeneity through outcrossing and/or interspecific introgression is more disadvantageous than in a site that is more varied edaphically and more varied with respect to herbivore challenges.

(c). Why don't those herbivores that can deal with the defenses of monoculture tree stands move into these habitats and literally mow them to the

ground? There is certainly no escape in space. There are herbivores that can feed on the vegetative and reproductive parts of these plants (e.g., Anderson, 1961). I suspect that the answers to these questions are in the following area. When the habitat first appeared, and various species of trees were specializing with respect to it, those that got mowed down when they occurred in pure stands probably dropped out of the race early on (they should still persist in mixed stands, however). Second, one of the traits for living in a habitat supporting a pure stand should be the evolution of those kinds of chemical and behavioral defenses so effective that the plant does not rely on escape in space; perhaps they are more expensive chemically, but then again perhaps they can be afforded owing to less investment in interspecific competitive ability (e.g., desert cacti). Third, these plants have escape in time, and they use it; in many species seed production is highly synchronized within the year and in many species, at supra-annual intervals (bamboo being the epitome; Janzen, 1976b). Owing to the extreme specificity displayed by many tropical seed-eating insects, the seed crop of the monoculture stand does not necessarily draw a guild of insect seed predators in the same manner as the flower crop may draw a guild of flower visitors from the surrounding mixed forest. However, such plants may also be involved in satiation of seed predators, and then they may draw large numbers of animals from surrounding areas and require long supra-annual periods to accumulate enough reserves for enough seeds to satiate these animals (e.g., bamboo, *Dipterocarpaceae*). The same process is likely to be operating with new leaf production. For example, in Corcovado National Park (Costa Rica), all trees of *Mora oleifera* drop their leaves in late November and put out a new synchronized crop in December.

SECONDARY COMPOUND CHEMISTRY AND HERBIVORES

This is undoubtedly the most actively expanding area in tropical (and extra-tropical) animal-plant interaction studies. It is easy to predict that the descriptive data and tests of hypotheses over the next ten years will make our current understanding seem amazingly primitive and naive. Take any paper on this subject in a current journal, and you can generate more questions with its data than it answers; and if not, just combine it with the next apparent test of the same hypothesis to get the desired effect. We are even still drowning in terminological difficulties, with specialist, generalist, secondary compound, herbivore, strategy, community, at the top of the list; at least we seem to have left niches by the wayside.

It is presumptuous for me to finger promising areas, but since asked, I will presume. As I mentioned earlier, do not jump on me for leaving out yours, just be happy that it is not yet a bandwagon. I will simply ask questions, the answers to which I feel are either as yet invisible or are only dimly visible.

(1). What sort of enzyme systems occur in the guts and livers of herbivores (e.g., Freeland & Janzen, 1974; Krieger et al., 1971), and can they be turned on and off so fast that an animal can move from one species of plant to another with hardly a pause? Yes (Brattsten et al., 1977). If they have them generally,

and can be so activated, why aren't all animals generalists that can feed on any kind of foliage?

(2). Is it true that large animals mix their foliage intake as a way of minimizing damage from any one secondary compound (dilution, antagonisms, keeping each compound at a low concentration), or do they do it largely for nutrient balance reasons (Westoby, 1974; Freeland & Janzen, 1974)?

(3). There is more foliage present of species that big herbivores are known to eat than they do eat; does this mean that they are not food-limited (Berwick, 1974), or does it mean that there are upper limits for even the acceptable items? Or does it mean that the critical times in food shortage (pregnancy, weaning, etc.) have not been examined?

(4). How do the metabolic costs of making secondary compounds (Penning de Vries et al., 1974) compare with the fitness costs of making them?

(5). At the habitat level, what is the structural array of secondary compounds? In other words, are defenses more heterogeneous within than between the food of herbivorous guilds (Janzen, 1973b; Feeny, 1976; Rhoades & Cates, 1976; Cates & Rhoades, 1977; Futuyma, 1976)?

(6). Why do many plant parts contain trace amounts of a variety of secondary compounds, and then a large amount of a few? Are they really sloppy or does this array present a more viable or effective defense against the more specialized or the more generalized animals?

(7). How would you design the optimal pathway for the production of a secondary compound? Example: minimize the number of places that enzymatic reactions are needed, maximize the number of times that the same enzyme can be used, canalize the substrate-product sequence such that its intermediate parts cannot be stolen from other pathways (but perhaps a really sophisticated system would allow borrowing?).

(8). Why are specialist animals specialized to only one kind of host (if they are); is it that detoxification systems are really that intersystem incompatible? Or is it like the canavanine system where the beetle is using that which is produced by the detoxification process (Rosenthal et al., 1977), and therefore we can state that the animal avoids other hosts not only because they are toxic but because they do not offer special dietary input.

(9). Why are sugars the molecules tacked onto large active molecules to render them inactive (e.g., lectins, Liener, 1976, and other glycosides)? Is it just because of the ubiquity of hydrolyzing enzymes in animal guts?

(10). Since insects have a much shorter generation time than do plants, why don't insects always come up with a resistant strain that eliminates the plant before the plant can evolve a chemical defense?

(11). What happens when we view cellulose as a secondary compound?

(12). If bacteria can degrade cellulose, lignin and other such indigestibles, why can't animals do the same?

WHY DO FRUITS ROT AND SEEDS MOLD?

The brewery's fermentation vats are not where yeast evolved ethanol produc-

tion and bread is not the native habitat of blue bread mold. An exploration of the biology of rotting fruits and molding seeds is likely to produce some very interesting and unexpected results, both here and in the tropics. When a microbe has found itself a ripe fruit, it has two options. It can begin using the resource rapidly and directly for its own growth and multiplication. On the other hand, it can do this somewhat more slowly and convert part of the resources into compounds which the anticipated vertebrate consumer of that ripe fruit will find objectionable, toxic, repulsive, etc. I suspect natural selection to have favored genotypes displaying the latter solution. The selection should be more intense the more rapidly the dispersal agents and fruit parasites remove the fruits from the tree, and the less fastidious are the frugivores. Seen in this light, a sour or alcohol-rich fruit is not just an accident of microbial metabolism or the detritus of microbe-microbe warfare, but may also be the explicit outcome of selection for avoidance of consumption of microbes (or insects) by vertebrates (Janzen, 1977f).

The same argument may easily be applied to the fungi whose hyphae grow over the surface of grain caches of man and other animals. Only here, they are protecting a much more valuable resource (higher nutrient content, lower abundance, large amount of work invested in harvest is a measure of work that will have to be repeated to reharvest it if lost, reserves for a resource-poor future, etc.). The protection will have to be more violent than for a fruit, and it is; aflatoxins, ergot alkaloids, and antibiotics may be used as examples. It is of particular interest here that both insects and vertebrates are susceptible to these compounds, and the only fungal hyphae that regularly make such nasty things are those that live on grain stores (Janzen, 1977f).

The biology of rotting fruit and moldy grain stores in the tropics is unknown in the wild and in most human habitats. Why do cassava tubers (*Manihot*) spoil so quickly that a major portion of the earth's cassava production land is serving as a storage bin because once harvested, cassava tubers have to be eaten? Another way to ask this is "Why do the spoilage organisms in cassava tubers so quickly render them unuseable for vertebrates?" Many species of tropical fruits are notorious for being poor at shipping and storage, unless picked extraordinarily green. Is this because the fruits are particularly susceptible to rotting organisms (owing to lack of selection for long half-life of ripe fruits owing to very active dispersal agent guilds), because tropical microbes are especially competent in their competition with vertebrates (owing to very active dispersal agent guilds), or a combination of the two? How long does a yeast clone have to make a tropical rain forest fig so sour that a bat will leave it on the tree? Perhaps it may have only one or two days at the outside. I should add that the opportunities for coevolution of competitive partners against the vertebrates is very great, and may take the form of teams of microbes and the insects that carry them from rotting fruit to intact ripe fruit. It is even possible that an exploration of some of these esoteric areas might well lead to pragmatic applications in the area of Ashton's (1976) proposals for exploitation of wild tropical fruit trees for their fruits.

THERE IS NO OPTIMAL SEED

The fitness of the female parent tree has to be measured in some way relevant to the number of new members she contributes to later generations and how well these new members do on the same parameter. The environmental challenges presented to her seedlings are varied and unpredictable with respect to any given seed (though the variation and relative abundance of environmental challenges may be quite predictable to the parent). There can therefore be no optimal seed size for any species of tree. A large seed may generate a very strong seedling, but it may be sorted out by the seed dispersal process so as to land in a poor site. A small seed may generate a puny seedling but regularly land in a heavily insulated site. This year, a female may have $\frac{2}{3}$ of her seeds land on dry sites and $\frac{1}{3}$ on wet sites; next year she may do the opposite purely because of interyear differences in weather. In view of these problems, I hypothesize that there can only be an optimal distribution of seed weights within a female's seed crop. If this is so, then the distribution of weights of seeds (or some other measure of the size of the bag lunch for the seedling) is not a simple outcome of sibling competition and physiological sloppiness by the parent plant, but rather may also be engineered by the adaptive value of having various proportions of the seeds in different weight classes. Incidentally, since the challenge to seeds varies from year to year, there may not even be an optimal seed size distribution in a crop; it will have to be within a lifetime.

Ateleia herbert-smithii, a caesalpinaceous legume tree in Santa Rosa National Park, Guanacaste Province, Costa Rica, may provide an example. Not only does this tree display 1.89-fold variation in the mean seed weights among trees, but within a crown there is 1.6- to 2.6-fold variation in seed weight. There are some cases where twins are produced in the normally single-seeded wind-dispersed fruits. Here, the pair of seeds has a combined seed weight greater than the mean weight of solitary seeds, but each twin weighs considerably less than the individual solitary seeds. This can be simply interpreted as the outcome of sibling competition. However, it could also be a mechanism for dropping some light seeds near the parent plant. A fruit with twins should fall in that part of the seed shadow that normally receives single-seeded fruits with heavy seeds. In fact, the production of twins may be adaptive simply in homogenizing the seed shadow (Janzen, 1977h). In the same vein, the 3.62-fold variation in seed weights found within a single crop of *Mucuna andreana* could well be adaptive in generating a more homogeneous seed shadow than if all the seeds weighed the same (Janzen, 1977g).

A small hard object moves through the digestive tract of an animal at a rate related to the object's volume, shape, specific gravity and (probably) surface texture (Hoelzel, 1930; Alvarez & Freeland, 1921; Hinton et al., 1969). It follows that if a vertebrate eats a distribution of seed sizes from a single crop, they are likely to come out in a different pattern than they went in. Further, the probability that they will go in at all should be influenced by these traits, as well as the relative seediness of the fruit. For example, does a tapir spit out flat 500 mg seeds more frequently than spheroidal 500 mg seeds of the same species? Does a deer chewing its cud spit out the large members of a seed crop and let the

small ones pass on through? Could the small seeds from the same *Enterolobium cyclocarpum* seed crop crack between the molars of a peccary more easily than the large seeds? Yes (Janzen & Higgins, 1977).

Once we put on this pair of glasses, interesting variation pops out all over the place. What is the meaning of variation in fresh ripe fruit weight within a tree's crop? Bonaccorso (1975) noted that different species of bats took *Ficus insipida* fruits of different weights from the same tree; this should generate a quite different seed shadow than if all the figs were of the same weight and thereby taken by only one species of bat. What is the significance of the spatial variation in fruit location in the crown? What is the significance of the temporal variation in fruit ripening times within the crown? What about the variation in seediness within a crown?

But do not forget the zygote. The world is not constituted solely by female parental manipulation. What is good for the parent is not necessarily good for the individual seedling. Once the zygote is formed, you might argue that it should do everything it can to extract as many resources as possible from the parent plant. Of course, the parent has many physiological ways of controlling this, but there may also be good reasons for the offspring to constrain its gluttony. For example, the very large seed may simply be spit out below the parent by the dispersal agent, and its less greedy sibs make a happy passage through the intestine to a distant light gap. The large seed may lower its fruit/seed ratio to where it is taken late if at all, and thus be killed by some seed predator taking what has been left behind by the dispersal agents. The individual zygote is not in the process of generating a seed shadow but rather in maximizing its own chances of survival to a highly reproductive adult; it has only one chance, the parent has many.

OPTIMAL MATE SELECTION

Animals are conspicuous in their courtship displays, fickleness, promiscuity, coyness, variably intense rape, and other descriptors of mate selection by both sexes. What are the analogous processes in plants? I would like to suggest that they are choice of pollinators, timing of flower presentation, duration and time of stigmatic receptivity, duration and time of pollen release, degree of separation of the sexes within and between conspecifics, abortion of ovules, and abortion of zygotes of a variety of ages. The core questions are "How many of which fathers does the female part of the plant genome want for any given seed crop?" and "How many offspring in which and how many seed crops does the male part of the plant genome wish to sire?" I would argue that in either case the answer is not a maximum number but rather some optimal number and optimal distribution. Further, I see no reason to believe that the optimal numbers and distribution of fathers and mothers are very likely to be the same for the female and male, and that the difference leads to such things as differential pollen acceptance, selective pollen presentation, monoecy, dioecy, etc. (Janzen, 1977a).

I suspect that the most unappreciated mechanism for shaping the genetic composition of her seed crop is that of zygote abortion. It is conspicuous that the individuals of a very large number of species of plants regularly abort all but a

very small number of the flowers that they produce. Flower to mature fruit ratios of 100–500 to 1 are commonplace in large tropical trees. Even careful hand pollination does not drive this ratio downward, though it can in certain species. Incidentally, I should note that pre- and post-zygotic abortion are probably not as different as they would seem since both should be controlled by the seed-bearing plant. The male portion of the zygote is certainly not going to be selected for abortion tendencies as it has all to lose and nothing to gain.

Since my focus is here on animal-plant interactions, let me list some of the ways they influence abortion of flowers and zygotes.

(a). By attacking a fraction of the ovules and zygotes in the flower and developing fruit, seed predators may render the fruit not “worth” the cost of further development or maturation.

(b). By being unpredictable in which flowers or immature fruits they will attack, and to a certain degree in how many, such animals require the retention of a large number of (perhaps) suitable flowers or green fruits from which the fruits to be matured can be selected after the animals have taken their toll (the excess flowers or fruits are then aborted).

(c). By bringing variable amounts of appropriate pollen (e.g., pollen that is not from yourself or a close relative) to the stigmas, the pollinators require the production of a large number of stigmas so that at least some minimum number get the right amounts of the right pollen; the flowers containing stigmas with the wrong pollen are aborted.

(d). Owing to the vagaries and resource-gathering behavior of visitors to flowers, a large flower crop may be necessary just to satiate visitors, to get the right kinds, and to do it in competition with other plants; these flowers are then aborted simply because insufficient resources can be spared to mature their seeds even if pollinated.

Viewing pollen donation and capture in the light of these comments brings me to the problem of the act of not setting seed by a flowering tree. With dioecious species, the lack of seed production by male trees has never caused the puzzlement it is due (but see Bawa & Opler, 1975, 1977). Dioecy is just a more final example of the behavior displayed by a tree with perfect flowers that likewise sets no seed. I would hypothesize that such trees, dioecious or hermaphroditic, have often made some kind of an internal decision that they will have a higher fitness by putting everything into pollen donation rather than into pollen capture and nursing zygotes. Medway (1972) recently commented on how “after flowering, invariably some species failed to produce fruit”; Grubb (1977) picked this up as “circumstantial evidence exists for massive failure of pollination in some species . . . in the lowland tropics”; it is commonplace for foresters to label trees that flowered but did not seed as having “failed” to reproduce. Quite the contrary, they may have reproduced much more heavily than the tree bearing seed, simply by having sired many seeds on that tree and others that did set seed. We don’t label an animal as having failed to reproduce because he doesn’t get pregnant after copulating.

There are at least two ways that animals may be responsible for morphologi-

cal or physiological dioecious behavior by plants, both of which deserve much more attention than they have received.

(a). If seed predators and their satiation are involved in the tree's biology, the tree reproducing by seed may have to produce a very large seed crop or none at all; here then, the highest fitness may be achieved by being solely a pollen donor when young, sick, or between large seed crops.

(b). Dispersal agents may not be accurate enough to put more than an occasional seed into a habitat in which there are enough resources to be a healthy seed-bearer, but may place many seeds in habitats that just barely allow adult survival. The plant, once dispersed to the latter habitat, cannot get up and walk to a better place, and thus may be doomed to be a pollen donor or nothing.

COMPLEX ANIMAL-PLANT INTERACTIONS

There are four complex animal-plant interactions about which we now know a fair amount: orchid-euglossine bees, figs-fig wasps, neotropical acacia-ants, and leaf-cutter ants. Their taxonomy is fairly well understood, the basic elements of the interaction are understood, and they have been widely publicized. On the one hand, it appears that there is little interesting new ground to be plowed with each, and therefore the bright young field naturalist should look for other systems on which to expend energy. I would contend the opposite. These systems are now prime for high quality field studies incorporating modern ecological and population biology thought; the student need not waste years doing their taxonomy and natural history just to determine where to start. I have not started such a new study with any of the first three, but by nibbling at their surfaces for just a moment, the following interesting areas appeared. The fourth is being heavily studied by several investigators and I will not dwell on it here (e.g., Rockwood, 1975, 1976; Cherrett, 1968; Martin, 1974; Lugo et al., 1973; Hubble, personal communication).

ORCHID-EUGLOSSINE BEE INTERACTIONS

(a). How many parasites of the system exist (analogous, for example, to *Pseudomyrmex nigropilosa* in acacia-ants (Janzen, 1975a) or to *Sycophagus sycomori* in *Ficus sycomorus* (Galil et al., 1970)? It is assumed that the bees that come to the orchids and to the scents put out to survey them are pollinators of one or more orchids. There is no biological reason why this has to be so. Even if the bee does pick up pollinia, there is no guarantee that it has the appropriate behavior and/or morphology to put it back in the right place. It is already recognized that a visiting euglossine may not be the pollinator, yet get chemicals from the flower (Dressler, 1968a; Dodson et al., 1969); however, there is no reason that such a bee has to be the pollinator of *any* orchid. However, there are obvious forces operating to set the carrying capacity of the habitat for such parasites, and this should vary with the number of species of orchids, the number of species of euglossines, their numerical relationships, seasonality, etc.

(b). Is the visitation of an orchid's flowers, in its natural habitats, habitat-

independent? Some observers have already noted that certain orchid bees will not come to baits or orchids placed in the open sun but will visit them in the shady nearby rain forest understory. I suspect that the story is much more complex than that, and much more interesting. In March 1977 I put five different chemicals (cineole, eugenol, methyl salicylate, benzyl acetate, and methyl cinnamate) out in five different forest types on the same day within a circle of 2 km radius in Corcovado National Park, Costa Rica. The numbers of euglossines that came to each site differed dramatically and the array of species differed somewhat, suggesting that if any given orchid were growing in one of these sites, its visitors could have been dramatically different. An orchid is not an orchid. Such differences should have dramatic effects on species packing in orchids, inter-habitat species richness of orchids, and the relative fitness of an orchid in a given habitat as compared with a conspecific in another nearby habitat.

(c). How much self-pollination occurs in hermaphroditic euglossine-pollinated orchids by the simple event of a bee picking up a pollinarium today and bringing it back tomorrow? At least one tropical orchid, *Encyclia cordigera*, is highly self-compatible (study in progress, Santa Rosa National Park, Guanacaste Province, Costa Rica). Since most adjacent conspecifics are probably closely related (orchid seed shadows are probably strongly peaked as in other wind-dispersed seeds), there is also likely to be an extraordinary amount of incest in orchid matings.

And if interspecific hybridization occurs *physiologically* so easily with orchids (Dressler, 1968b), does this really mean that they have extremely faithful pollinators as is generally assumed, or does it mean that orchids live in a world where it is very profitable to steal genetic information as whole blocks or as proven mutations from other genomes? If they do the latter, then I expect strong selection for the ability to obtain this information without severe perturbation of the phenotype. The conventional means for detecting hybrids, the means that are used to say that orchid hybrids are very rare in nature, might be therefore of little or no use.

(d). An orchid female generally has fewer fathers for her clutch than does a member of any other family except perhaps the Asclepiadaceae (and speaking of which, what do orchids and asclepiads ecologically have in common so as to have generated their convergence on this axis?). Every orchid fruit, with its hundreds of thousands of seeds, has but one father. Depending on the behavior of the orchid bees and the density of orchids in the area, even if there is more than one pod per plant, it is possible for multi-podded clutches to have only one father. At the very most, the ratio of fathers to seeds has to be on the order of a very few to hundreds of thousands. In what way could this observation be related to the point made in the last paragraph of the previous section?

FIGS-FIG WASPS

(a). Since no one has ever done anything but rear the fig wasps out of syconia (and none of that has been done in a quantity any greater than that needed for taxonomic purposes) (Hill, 1967; Ramirez, 1970a), there is no infor-

mation on what kind of interspecific pollen is being carried *into* a fig crop. Again, the literature loves the statement that hybrids of figs are very rare (e.g., Hill, 1967); however, since there is only one experimental cross on record (Condit, 1950) how is one to know what a hybrid fig looks like? An extensive examination of the remains of the female fig wasps inside a large number of recently pollinated but still quite immature syconia would tell how much foreign pollen is getting into the system at each generation.

(b). Female fig trees pay offspring for pollination. Fig wasps are seed predators. There is no published study of the intensity of this predation, but one in progress shows 30 to 50% for three fig species. What is the possibility that one of the selective pressures favoring gynodioecious figs (one morph of the population has syconia with solely female florets with styles too long for oviposition) is the act of obtaining the services of the wasp without paying the cost in zygotes? What is the overall cost in zygotes per intact seed for monoecious as compared with gynodioecious fig species?

(c). Who eats figs? Everybody does. Nonsense. Yes, there are fig species that produce large numbers of small figs that are taken by a very large disperser coterie. These species must have very homogeneous seed shadows (generated by birds, bats, pigs, primates, etc.). On the other hand, there are fig species that seem to be largely visited by a very select subset of the frugivores in the community (e.g., *Ficus ruginervia* produces large figs apparently taken only by gibbons, siamangs, and two species of squirrels when growing only a few meters away from *Ficus sumatrana* which was visited by at least 25 species of birds and 9 species of diurnal mammals—to say nothing of bats, which were apparently unrecorded; McClure, 1966). Morrison (1975) noted that the ripe figs of several species of Barro Colorado Island figs were taken largely or exclusively by bats; the howler monkeys are the only other visitors mentioned, and they appeared to take largely immature syconia. It is my guess that they took almost entirely immature syconia.

I suspect that the traits of ripe fruits are engineered by the need to keep them out of the wrong dispersal agents as much as to get them into the right ones (and see Howe, 1977). There should be many parasites present in any disperser-fruit system. The trick is recognizing the parasites (as separate from the seed predators) because they do their damage by putting the seed in the wrong place, rather than by killing it directly. The neotropical oil birds (Snow, 1962) come to mind as the most glaring example, since it appears that many of the seeds they eat are later regurgitated in a cave where they die. Likewise, a Mexican oriole that eats the fruit pulp around *Acacia cornigera* seeds and drops the seeds below the parent tree may have killed those seeds as dead as if it had ground them in its gizzard. It appears that *Andira inermis* fruit pulp may contain an antibiotic which thereby renders it a high quality food item solely for those animals that depend little on bacterial degradation for the extraction of nutrients from their food (Janzen, 1977e). It occurs to me that the various bat-dispersed figs on Barro Colorado Island may be doing the same; interestingly, such a compound might also be functional in slowing the rate of spoilage of a fig that has already been opened to the outside world by the exit of the fig wasps. If this

hypothesis is correct, then consumption of green figs before such a compound is activated might be the only way that a howler monkey can eat them, since it depends heavily on its bacterial community for degradation of foliage. Howler monkeys often avoid ripe fruits but eat the same species when green (Glander, 1975a, 1975b, 1977).

(d). The current consensus seems to be that fig wasps are very host-specific and that the figs are strongly synchronized within a given crown (Ramírez, 1970b; Hill, 1967). I have no doubts that this is the case for many species in many habitats. However, Ramírez (1970b) has already pointed out that on islands there may be selection for the loss of synchrony within a crown if the fig population is so small that there could be times when no tree is in a receptive state. There should be other habitats where both the host-specificity and the synchrony should break down. Butcher (1964) stated that the two native species of *Ficus* in Florida, *F. aurea* and *F. laevigata*, are pollinated by the same species of wasp, *Secundeisenia mexicana*. If this should occur anywhere, it should be Florida with its killing frosts. McClure (1966) noted that in the dipterocarp forests around Ulu Gombak there was a two month progression of ripe figs through the crown of a *Ficus sumatrana* (and shows it in the graphs for two other species as well). Fig wasps take about a month for a generation. Unless the pollination is synchronized but the syconial ripening grossly asynchronous, there is a very great possibility of self-pollination in these species of figs. At least two selective pressures could be operating to produce asynchrony within the crown. First, it may be that fig tree density is generally low in this forest, perhaps even as low as on a small island from the viewpoint of the wasps. Second, it may be that the actual biomass of fig-removing animals is small, and if all the figs this tree can make in a pulse were to be matured in a week or two, most would rot on the tree or the ground for want of not having been removed (the frugivores having been satiated).

ACACIA-ANTS

(a). There is no wild plant species anywhere in the tropics for which even an approximate herbivore load has been described. If the ants are removed from neotropical swollen-thorn acacias, the herbivores that normally feed on them and those that feed only on the largely undefended plants often become temporarily abundant and easy to census. Combined with careful observations of the insects feeding on acacias with their colony intact, it would be possible to not only rapidly identify the herbivore load of at least one plant species, but to ask how it behaves when the defenses of the plant are suddenly removed without physiologically altering the plant. When my early ant-acacia studies came out, there was a good deal of "Oh My" of how all those little ants could do such a marvelous job of defending the tree. The significance of those studies lay not, it seems to me, in this aspect. Rather, here we have a plant that in nature can be deprived of its defenses and thereby demonstrate how important are its defenses in determining the amount and structure of the herbivore load.

(b). When an ant-acacia is crossed with a non-ant-acacia, the offspring are most amazing organisms. They have either Beltian bodies, large to normal

thorns, large nectaries and seem to be poorly protected, or they almost entirely resemble the non-ant-acacia parent. Thus it is as though the ant-acacia traits were one gene (and you get an ant colony as well). If this gene is donated through interspecific introgressive hybridization, a non-ant-acacia may become an ant-acacia. It does this without ever losing its other traits which, for example, would cause it to be placed in a quite different subgroup of the genus. It would then appear that the ant-acacia interaction had evolved independently on several different occasions. The 10 or so species of neotropical ant-acacias seem, on the basis of flower and fruit traits, to belong to quite different species groups (Janzen, 1974d). The system is wide open for experimental verification. And what would it mean to attempts to reconstruct phylogenies based on suites of traits?

(c). There are three species of obligate acacia-ants in Guanacaste Province, Costa Rica, that protect the common swollen-thorn acacia, *Acacia collinsii* (*Pseudomyrmex belti*—black; *P. nigrocincta*—the smallest of the three and with a yellow body with the gaster held straight out in back; *P. ferruginea*—rust red with the gaster commonly curled under the posterior part of the thorax). They all eat the same thing (Beltian bodies and foliar nectar), live in the swollen thorns, and aggressively protect the plant. All three occur in every habitat I have ever sampled. No large colony will cooccur in the same acacia with another colony. All colonies have but one queen, and while many queens may start out in the same acacia seedling, the winner takes all. It is hard to imagine a more monomorphic resource than ant-acacias. I suspect that originally one species was a specialist on the ant-acacias in the forest understory (*P. nigrocincta*), one species was a specialist acacia growing in open but moist sites such as river edges and marsh edges (*P. belti*), and one species was a specialist on acacias growing in fully insolated but very dry sites (*P. ferruginea*). When the pasturing, cropping, and timbering broke up the habitat structure, all three species moved into each other's habitats and are found there today. In contemporary habitats the ratios of the species vary widely among habitats, and I suspect that in the original habitats there were always a few colonies of the other two along with the most abundant species. The colonies can be moved about, the acacias can be seeded with queens, and all occur in large numbers. The opportunities for experimental study of direct competition between sessile animals in terrestrial community are enormous.

(d). The pulp around the seeds of *Acacia collinsii*, moist when ripe, can be placed in a plastic bag, sealed, and left for a year without spoiling. From what I said earlier about bats and *Andira* and fig fruits, there is one obvious suggestion about what it contains. All swollen-thorn acacias have seeds imbedded in a sweet pulp (Janzen, 1974d), apparently for seed dispersal by birds (in contrast, I know of no neotropical non-ant-acacia with this trait). Presumably this trait arose many times independently. What a marvelous opportunity to study convergence in fruit protection traits.

The above hypotheses and systems briefly alluded to for orchid-euglossine bees, figs-fig wasps, and ant-acacias are, I am certain, only a tiny fraction of the studies that can be developed into large and clean studies in coevolution, popula-

tion biology, gene flow, competition, etc. These suggestions are possible because some background has now been developed for these systems. Yes, the "Oh My" part of the studies has been killed rather dead; now it's time to start on the interesting things.

ONE LINERS

(1). Why do trees have rotten cores? Hypothesis: to provide a place, through the removal of unneeded structure, for animals to roost and defecate and for microbes to grow, which in turn generate a nutrient pool for the tree's roots. The actual process should be through the selective and only temporal protection of the core of the heartwood from decomposers (Janzen, 1976c; Fisher, 1976; Thompson, 1977).

(2). Why do vertebrate dispersal agents leave the tree to eat the fruit they have picked? Hypothesis: because there has been strong selection for chemical, morphological, and behavioral traits of the parent tree to be an objectionable place to perch. The competing hypothesis is that the fruiting tree is a focal point for foraging carnivorous predators.

(3). Why don't the ants of the world take over the flowers of the world and protect their nectaries just as they do extra-floral nectaries (even on those on the outside base of the flowers)? Hypothesis: there is an anti-ant compound generally present in floral nectar. And in case you still think nectar is just sugar water, read recent papers started off by the Bakers (Baker & Baker, 1975; Baker, 1975).

(4). Why do rain forest seedlings with mycorrhizae recover from herbivory much better than do conspecific seedlings that have not yet acquired (accepted?) a mycorrhizal association? Hypothesis: the seedling can mark time waiting for the appropriate fungal associate using only its seed reserves plus the very small amount of resources it can harvest in the heavily shaded rain forest understory, but if it has to undergo the major capital investment of replacing lost photosynthetic structures, it does not have adequate resources (Janos, 1975).

(5). Why do rain forest understory shrubs contain a high amount and diversity of so-called trace elements (boron, cobalt, etc.; F. Golley, personal communication). Hypothesis: the heavily shaded rain forest understory is one of those resource-poor habitats where chemical defenses are of utmost importance (Janzen, 1974b); large quantities and many kinds of secondary compounds may require large quantities and many kinds of co-enzymes for their protection, and co-enzymes normally contain a molecule of a so-called trace element.

(6). What is the distribution of intensity of seed mortality by animals among the members of a tropical tree population? Hypothesis: there is a very skewed distribution, with most individuals producing few or no surviving seeds, and a very few producing most of the members of the next generation. If this is verified, then the opportunities for rapid genetic change and the selection for high levels of information exchange among members of the population should be very high.

(7). What do whole disperser coterie, herbivore loads, and suites of pollinators for an individual and a population look like? Hypothesis: they will be

rich in species that parasitize the system, rich in species that gain resources but take so little that the mechanisms to remove them would cost much more than the value of what they take, have a few key species that drive many of the traits of the system, treat individuals very differently even within populations of closely adjacent individuals, and display strong competitive interactions through the medium of the plant (Janzen, 1973c), as well as directly with each other.

(8). Why are grasses so edible? Hypothesis: they are involved in satiation of leaf predators (being possible by having put the high investment centers underground where they cannot easily be reached by fire and herbivores); the cost of chemical defenses would generally be higher than the fitness loss that occurs through the grazing that is produced by the animals that make it from one rainy season to the next (and see especially Sinclair, 1977).

(9). Are plant apparency arguments (Feeny, 1976; Rhoades & Cates, 1976) applicable to all parts of plants, as they appear to be to foliage? Hypothesis: probably, but it will require some very careful definitions of what is apparent and what is not. For example, at least two major groups of mast-seeding trees, oaks and dipterocarps, have polyphenolics as their major chemical defenses (if any be). A very large number of trees that do not display habitat-wide supra-annual synchrony of seed production have alkaloids and other conventional toxins in their seeds. One could argue that the seeds of mast-seeding species, widely spaced in time, are less apparent than the seeds of tree species that fruit or seed every year. However, I could rebut this argument by noting that when the mast-seeders do seed, they do it in such abundance (and often in such pure stands) that the seeds are enormously apparent; on the other hand, species of seeds defended by alkaloids, etc. are often very widely scattered or rare, and thus much less spatially apparent, even if they fruit every year. In closing this section, I must note, however, that many species of seeds contain both direct toxins (alkaloids, uncommon amino acids, cyanogenic glycosides, etc.) and digestion inhibitors (tannins, lectins, protease inhibitors); e.g., chocolate beans contain tannins and 3 kinds of alkaloids. Perhaps it is that as the nutrient content per bite of food rises, the adequacy of only one class of defense in the plant part declines precipitously.

(10). Why is the biomass of palms in Africa so low? The exceptions are oil palm (*Elais guianensis*) and raphia palm (*Raphia taedigera*) pure stands in swamps, borassus palms in very arid areas (e.g., Samburu National Park, Kenya), and very thorny climbing palms in swampy rain forest. Richards (1973) has already noted that Africa has a ridiculously low number of species of palms—about 50 species as compared with about 1,140 in the neotropics and 1,150 in the Asian and Australasian area. Hypothesis: palms, with their single large growing points, are particularly susceptible to herbivory by elephants, mammals which were until recently prominent browsers in African forest habitats.

(11). Can the fitness of a plant be raised by herbivory, thereby selecting directly for palatability or lack of defenses in a plant part? This hypothesis has recently been championed by Hendry et al. (1976), Owen & Wiegert (1976), and Harris (1973), among others. Aside from the obvious cases of seed dispersal and pollination systems, and the problems of defenses in these systems being incom-

patible with “allowing” herbivory by the “appropriate” animals, I have yet to see a convincing case of a positive answer to this question. Of course, an herbivore may remove a part that would otherwise have to be actively dehiscenced by the plant, or turned off by the plant, but to put such an activity in the hands of the herbivore requires that it will only do that and that it will be reliable in its activity; that is to say, the plant loses part of the control over itself. In the most dramatic case, mild defoliation of crop plants may result in overall increased yield per field (Harris, 1973). However, this is quite easily explained by assuming that the defoliation breaks apical dominance, something that would result in loss of status in the natural competitive situation, but is optimal for properly spaced plants in the field situation. The same applies to cases where mild browsing of bushes appears to raise their vegetative productivity, and when mild defoliation of a wild plant increases its seed production (e.g., Cavers, 1973). In short, just because a person runs faster after hitting a wasp nest, we do not conclude that (a) being stung raises your fitness and (b) susceptibility to being stung is a mechanism evolved by humans to get themselves to run. Finally, I can simply state that the various schemes frequently proposed for the “value” of herbivores to the ecosystem at recycling leaf contents are evolutionary nonsense. There is no evidence that a plant gains more from having its leaves eaten and then (perhaps) taking up some of the mineral contents of that leaf or feces from the litter below than from keeping its leaf intact in the first place.

(12). Are extant gymnosperms and other “primitive” plants really freer of herbivores than are angiosperms (Regal, 1977)? If so, is this due to their secondary compound chemistry or is it due to accidents of host location by herbivores? Are we seeing the bare remnants of a once great flora being pushed out by the combined actions of herbivores and competition from plants with a superior growth form?

(13). Prominent and severe defoliation by highly host-specific Lepidoptera and Coleoptera occurs during the first 1–2 months after the rainy season begins in the Costa Rican lowland tropics (see Rockwood, 1973, for examples of its effects). Hypothesis: the cessation of defoliation after a single generation of a given species of herbivore is due to the accumulation of secondary compounds (such as digestion inhibitors, see Feeny, 1976) in maturing leaves which makes them unavailable to the insects. The corollary of this would be that a tree is susceptible to this event only because it has to make a new crop of leaves each year. Opposing hypothesis: the cessation of defoliation after a single generation of herbivores is due to a buildup of parasites and predators at this time of year. There is no direct or circumstantial evidence to support this hypothesis.

(14). New leaf-cutter ant fungus gardens are established by vegetative propagation from cuttings carried by the newly mated queens. Hypothesis: over many generations of leaf-cutter ants in an area, all the colonies will eventually be owned by the same subdivided individual fungus, which should in turn be the genotype that does best on that particular mix of plants which are available to the ants. This then becomes the world’s largest fungus and uses armies of leaf-cutter ant colonies to feed itself; will this result in manipulation of the colonies at a density and degree of intercolony aggressiveness which is suboptimal

for the ants and optimal for the fungus? Does this mean that leaf-cutter ants are more finely tuned to a habitat than expected, and therefore will also have more than the expected difficulty in colonizing new habitats?

(15). It appears that the species richness of herbivore loads of perennial plants reaches an asymptote within a few hundred years after the species has been introduced, with the level set largely by the areal extent of the population (Strong et al., 1977). Hypothesis: this conclusion will be most robust with highly apparent plants that are generally defended by digestion-inhibiting chemicals, since it is these plants that will have the most in common with those native plants that are fed on by generalists; newly introduced herbaceous and other plants defended largely by more direct toxins should require considerably more time to accumulate a normal herbivore load from the indigenous pool, as this will require evolution on the part of local herbivores (Gilbert, 1977). Herbaceous crop plants, however, will not be a useful test of this hypothesis; they have had their defenses bred out of them to various degrees and thus should quickly accumulate their saturation herbivore load. I should also note that a newly introduced wild plant will not likely occur in a major monoculture, as is the case with crop plants. Therefore, requirements of herbivore coevolution with the host's physiological behavior, size, phenology, etc. may become much more important in slowing the rate of accumulation of the herbivore load than Strong et al. (1977) found to be the case with crop plants.

(16). On 11 August 1977 a healthy male tapir swallowed 95 intact seeds of *Enterolobium cyclocarpum* and 80 intact seeds of *Cassia grandis* (weight about 0.7 and 0.5 g each, respectively); for the following six days there was no trace of these extremely hard seeds in the tapir's feces except for two *E. cyclocarpum* seed coats. Hypothesis: the seeds were sufficiently slowed in their passage through the tapir's digestive tract such that they were sufficiently softened such that they were digested rather than dispersed. The various eddy currents (e.g., loops in the intestine) and pockets (e.g., caecum) could thus be highly adaptive in aiding digestion of seeds too hard to break with the teeth. Furthermore, large animals commonly thought to disperse hard legume seeds may well be extracting a high price in seed predation; there have never been studies of what percentage of the seeds ingested actually survive the voyage through the animal.

IN CLOSING

I cannot resist commenting on the classes of administrative effort that I feel we lack in tropical animal-plant studies. First, I feel that we have quite enough hypothetical biology on the books. We desperately need information on the pragmatics of what is actually happening out there. I can generate, with a little help from my friends, a computer model that will predict anything; for example, a model can predict that increased productivity should increase species richness and that increased productivity should decrease species richness, or it can predict that a predator should increase its specificity as prey gets scarce and that a predator should decrease its specificity as prey gets scarce. It all depends on what natural history facts you plug into the assumptions. Let's go out and get those facts, and ask what is their frequency distribution among real mem-

bers of real habitats and guilds. Of course, we should be gathering the facts in respect to questions, but let's not let the airy-fairy castles in the sky block out the sun.

Second, many kinds of tropical animal-plant studies involve systems with patterns or cycles that will not be apparent until tens of years of data on the same individuals in the same habitats by the same investigators have accumulated. Funding for more than three years, and often more than two, is largely nonexistent unless you pay for it out of your own pocket. NSF states that they cannot tie up funds for long periods. Well, if NSF will give me \$40,000 in direct costs to spend this year, there is no reason why it should not give me \$40,000 in direct costs to spend over the next ten years in \$4,000 per year bits. They have paid out the money the first year and that is that. I would like to explicitly appeal for the establishment of grants of that structure, grants that will float with the investigator wherever or whenever transient. There are many long-term studies that I am now setting up for the last 30 years of my research life that could have had another 12 years on them had this sort of funding been available for this explicit purpose in 1965. Without this funding, we have the ironic situation that the shorter the time I have left to do research, the more likely my funding is to be sufficiently secure that I can set up such studies without having to worry about having the funds to census them annually.

Third, I would like to repeat a call (Janzen, 1977e) for some kind of internationalized and centralized chemical identification service, analogous to the great museums and their contained identification services. Secondary compounds and nutrient analyses of plants are to animal-plant interactions what Latin binomials are to ecology and evolutionary biology. A contemporary tradition is developing whereby natural products chemists are being prevailed upon with ever-increasing frequency to do secondary compound determinations by ecologists and evolutionary biologists. And in a manner exactly analogous to whole-organism taxonomists, the natural-products chemists are being swamped. With a very few exceptions, and these exceptions tend to have a very short half-life for obvious reasons, their work is slow, interrupted, variable in quality, and heterogeneous in coverage. Their primary commitment is not to those field biologists who send in a box of this or that at highly unpredictable intervals. Virtually all identifications are done gratis as a personal favor. When there is more than one class of secondary compound in the plant part, and this is normally the case, the specialist concerned can readily isolate and identify within only one class. It is as though I had sent a tanager gut off to a museum and the determinations came back reading 15 *Solenopsis geminata* subsp. *goofus*, 12 creepy-crawlies, 14 slimies, 1 blob, and 102 hardies. There is no Museum of Secondary Compounds nor is there any laboratory in the world that for a routine service charge will survey plant samples for kind and concentration of secondary compounds.

Yet if entomologists, ornithologists, primatologists, ecologists, etc. are to give secondary compounds the attention that they have long deserved in understanding animal-plant interactions, such an identification service is essential. I am certain that the highly inconclusive nature of the tens of thousands of pages of

data that have been gathered on feeding biology of herbivores is largely due to (1) the impossibility for humans to identify secondary compounds with their own senses, and (2) the difficulty of getting such compounds identified by other workers. I have seen much evidence that field workers would be quite willing to conduct the feeding experiments and observations to place secondary compounds in their proper perspective if they could get them identified easily.

If connected with the appropriate institution, I suspect that such a laboratory could be established for less than 1 million dollars, and I suspect that its running costs could be largely met through charges for determinations. A spin-off would be research on the new compounds encountered and the purification (at cost) of large amounts of certain compounds to then be used in field trials. Such a facility won't happen unless some small and dedicated body of people take it on (e.g., people centered around E. A. Bell, King's College, London; T. Mabry, University of Texas, Austin; P. Waterman, University of Strathclyde, Glasgow; R. Cates, University of New Mexico), and they won't take it on unless ecologists and evolutionary biologists can create a climate in the funding agencies for its support.

So in conclusion then, where are the promising new areas in tropical animal-plant biology?

(1). Take systems that are already very well known in terms of general natural history and taxonomy, and apply current concepts of ecology and population biology to them, rather than picking on one of the many largely unexplored "Oh My" systems.

(2). Figure out how tropical plants survive in pure stands, rather than worry about the mixed species stands.

(3). Use the organisms to tell you about the rates and kinds of harvestable productivity, and work backwards from this to expose the underlying causes; again, for the mercenary at heart there may be some powerful lessons here on how to competitively exclude our competitors or increase the yield from apparently low productivity sites (e.g., a rubber plantation may be such an example, discovered quite accidentally).

(4). Apply the multitude of hypotheses and ideas that are appearing in secondary compound chemistry to tropical plants and the animals that feed on them. Do not be too fascinated with the generalities; let's get some frequency distributions of results first. Furthermore, it won't happen unless we can get some sort of an International Museum of Secondary Compounds, Isolation and Identification.

(5). Stop thinking in terms of optimal seeds, fruits, flowers, reproduction times, seed crop sizes, etc. We have to start thinking in terms of optimal distributions in space and time for these parameters (as well as for other parts of plants and animals). Most plant parts are confronted by a set of animalian challenges or mutualists, not just one.

(6). At the risk of being labeled a Darwinist fanatic, I would emphasize the value of looking very hard for the adaptive significance of traits that we regularly take for granted (e.g., variation in seed size within a seed crop, rotting of fruits, duration of ripening times for fruits, seediness of fruits). It has been

my general experience that pessimism about the adaptive significance of a trait is strongly correlated with ignorance of the natural history of the organism.

(7). All the contemporarily fashionable ideas about parental investment, optimal parentage, sibling rivalry, etc. all apply to plants as well as to animals. In the tropics, animals play an enormous role in plant breeding systems and much of their obscure interaction with plants may become clearer when we come to understand what are the driving forces that determine which plant is to mate with which plant.

(8). We need much, much more natural history of tropical plants and how they interact with animals. I don't mean miscellaneous field notes of which beetle was found sitting on which plant, but rather natural history directed at interesting questions in ecology and evolutionary biology; we have plenty of them.

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